Echolocation calls of Malaysian bats

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Abstract

The echolocation calls of free-flying bats of the genera *Tylonycteris, Glischropus, Hesperoptenus, Myotis, Emballonura* and *Taphozous* were recorded in the field and examined in their pattern of frequency change over time (fig. 1, 3). Except *Myotis hasseltii* (pure frequency modulated calls) the calls of all vespertilionids consist of a frequency modulated beginning and a nearly constant frequency end (fm-cf-calls). *Hesperoptenus blanfordi* emits alternately signals with different cf-parts (32 and 40 kHz). The function of this behaviour is discussed especially with regard to the range of the echolocation system. The species of the genus *Taphozous* show like all other members of this genus studied so far nearly constant frequency calls. Additionally to the strongest first harmonic here the fundamental and higher harmonics can be observed. The calls of *Emballonura monticola* are also only weakly frequency modulated.

Introduction

The echolocation of bats represents one of the very few active orientation systems used by animals. Additionally to the commonly observed adaptations of sensory organs to environmental conditions here adaptions on the transmitter side are to be expected, too. Examples from morphology are the complicated nose-leaves of many Rhinolophidae and Phyllostomidae. They are most probably used for beaming the sound in certain directions. Many details of their structure, however, remain unexplained.

Adaptations to ecological conditions are also found in the echolocation signals themselves. Depending on foraging sites and strategies (e.g. close to vegetation, in open space) calls of completely different structure are used (Neuweiler 1983; Habersetzer 1986). To understand the regularities involved the sonar signals of many species living and hunting in different habitats have to be examined together with detailed studies of flight and echolocation behaviour of single species.

Up to now only the echolocation calls of bats living in temperate zones have been studied relatively thoroughly (Europe: Ahlen 1981; Weid and v. Helversen 1987; North America: Fenton and Bell 1981; and many other studies). From tropical areas, rich in bat species, however, few observations are available. Detailed, comparative studies of free-flying animals have been carried out only in India (Neuweiler 1983; Habersetzer 1986), Zimbabwe (Fenton and Bell 1981) and Australia (Fenton 1982).

In the following the echolocation calls of 8 species (6 genera) of the families Vespertilionidae and Emballonuridae are described. Except one they occur syntopic in Ulu Gombak, Malaysia. Two genera *(Glischropus, Hesperoptenus)* have never before been studied bioacoustically, species of further two *(Tylonycteris, Emballonura)* have been recorded only hand-held or flying in the laboratory (Novick 1958; Grinnell and Hagiwara 1972), where the call structure is very different from signals used during foraging.

Methods

Most bats (exceptions see below) were observed and captured (with mist nets) between Feb 28th and Mar 24th 1984 at the Ulu Gombak Field Study Centre (3°20′ N, 101°46′ E) of the University of Malaya near Kuala Lumpur. *Myotis hasseltii* was captured at Kuala Selangor, *Taphozous melanopogon* was observed at the Batu Caves (further details see HELLER and VOLLETH 1988).

The echolocation and social calls were recorded with a self-built condensor microphone (similar to e.g. QMC SM1) and amplifier on a modified video recorder. With this combination frequencies up to 200 kHz could be registered. The frequency response during recording, however, was not exactly known and certainly not flat over the whole range.

Due to this microphone characteristic, the frequency-dependent atmospheric attenuation of sound (the higher the frequency, the stronger the attenuation) and different distances of the flying animals, no definite statements can be made about sound pressure levels. This holds true also for the relations of sound pressure level between fundamental and harmonics resp. between harmonics, and for the highest detectable frequency at the beginning of the call in steeply frequency modulated calls. It will be lower with increasing distance, even if the call emitted by the bat does not change.

If possible the frequency of constant frequency parts is used for characterizing a species. In the Vespertilionini with cf-call endings one has to consider that in short calls the frequency of short calls is higher than that expected from shortening longer calls (WEID and v. HELVERSEN in prep). Additionally inaccuracies result from the Doppler effect caused by the flight velocity of the bat. In *Saccopteryx bilineata* (cf-frequency 47 kHz) it comes to 2–3 kHz (PYE 1978) for example.

For evaluation, certain sequences were recorded with a RACAL store DS tape recorder and after appropriate slow down (mostly 32×) analysed with a MOSIP-FFT-processor (Fa. MEDAV, D-8520 Erlangen-Buckenhof, Am Tennenbach 9). Some original prints are shown in fig. 5 (echoes and background noise eliminated with opaque white), for fig. 1 and 3 the signals were copied by hand.

Results and discussion

Family Vespertilionidae

Nearly all analysed calls come from captured and identified animals after releasing.

Members of the tribe Vespertilionini

The four species of this group *Tylonycteris pachypus, T. robustula, Glischropus tylopus, Hesperoptenus blanfordi* were frequently caught simultaneously (see fig. 1 in HELLER and VOLLETH 1988) in the same mist net. *Glischropus tylopus*, however, was rarer than the other three species. More detailed observations of the hunting behaviour are not available. All species show the tribe typical fm-cf-call structure (WEID and v. HELVERSEN 1987): a steeply modulated beginning (fm-part) is followed by a part in which the frequency decreases only very slowly (cf-part). The portion of each component varies widely according to the situation: during prey capture and close to obstacles the cf-part is reduced (up to complete disappearance), in open environments however almost pure cf signals can be used.

Additionally to the fundamental frequency, harmonics (mainly the first and the second) can be discerned. Nothing can be said, however, about their amplitude in relation to each other and their meaning (see Methods).

Tylonycteris pachypus (Temminck, 1840)

In the calls (duration 2–7,5 ms) of three animals examined the highest frequency at the beginning was found to be 125 kHz. It sweeps down to 58 kHz in short calls without distinct cf-part and to 50 kHz in long calls (fig. 1A). During a prey capture situation, which was assigned to this species on account of the preceding calls, no frequency shift at the end of the final buzz as in *Glischropus tylopus* (fig. 1H) could be observed (fig. 1F).
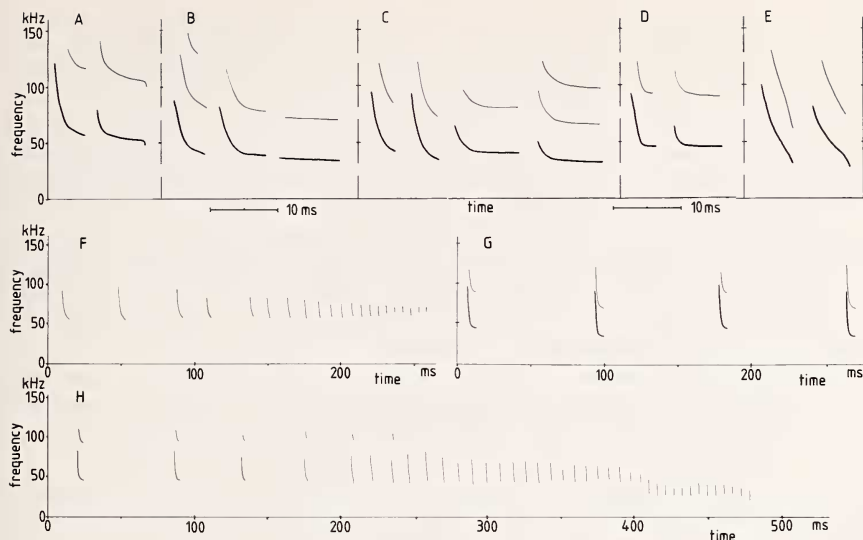
Fig. 1. Single echolocation calls of A: *Tylonycteris pachypus;* B: *Tylonycteris robustula;* C: *Hesperoptenus blanfordi;* D: *Glischropus tylopus;* E: *Myotis hasseltii;* F: feeding buzz of *Tylonycteris pachypus;* G: sequence of alternating high and low calls of *Hesperoptenus blanfordi;* H: feeding buzz of *Glischropus tylopus*

Tylonycteris robustula Thomas, 1915

The calls (duration 2–8,5 ms) are similar in their structure to *T. pachypus*, but lower in frequency. They start frequently at about 90–100 kHz and sweep down to 48 kHz in short and 40 kHz in long signals (fig. 1B). In very long calls the frequency may reach 35 kHz. The pattern of the frequency modulation is relatively variable (16 animals studied).

The intervals between the calls show a sharp peak between 70 and 80 ms and a broad side peak at about twice that time (fig. 2). In some sequences one can easily observe that sometimes calls are omitted so that the call interval doubles.

Glischropus tylopus (Dobson, 1875)

In contrast to the *Tylonycteris* species here the frequency sweeps at the beginning are very steep and do not vary much (3 animals examined). The length of the following cf-part (call duration 3–7 ms) is variable, its final frequency, however, relatively constant. The call starts at about 95 kHz, the frequency of the cf-part lies between 45 and 49 kHz (fig. 1D). Only in final buzzes calls of deviating structure can be observed. Fig. 1H shows an unusually long feeding buzz. In its last calls a frequency shift downwards can be observed as it is known from several other Vespertilionidae (e.g. *Pipistrellus kuhlii* SCHNITZLER 1984). Another final buzz of the same animal is considerably shorter and lacks such a frequency change.

Hesperoptenus blanfordi (Dobson, 1877)

Unusual for Vespertilionidae, this species shows two call types with similar frequency modulation but different frequencies, which frequently change in a regular way (fig. 1G). This alternation could be heard in 9 of 11 animals after releasing, in the remaining two only high frequency calls could be observed.

The high frequency pulses (duration 3–9 ms) started at about 105 kHz at the maximum and ended between 40 and 45 kHz, the low frequency calls (duration 3–10 ms) started also

at 105 kHz, but swept down to 31–37 kHz (rarely in short calls only to 40 kHz). The difference in frequency between two successive calls was 8+ 1,5 kHz (x+ SD; range 5–11 kHz; n = 28 pairs). Alternation occurred in short and long calls (s. fig. 1C), mostly, however, in a given pair the higher call was a little bit shorter than the lower one.

An alternating change between two call types is until now known only in some Emballonuridae (PYE 1973) and *Barbastella barbastellus* (AHLEN 1981). In *Nyctalus noctula* frequently call pairs can be observed with the first call being higher in frequency than the second (MILLER and DEGN 1981; AHLEN 1981).

In emballonurids PYE (e.g. 1973) assumes that alternating is used as a certain Doppler effect compensation. The frequency difference of 2–3 kHz found there does not disprove this hypothesis saying that the echo of the low frequency call is received at the frequency of the higher call. A difference of 8 kHz, however, would require extremely high flight speeds never reached by *Hesperoptenus blanfordi*.

In view of the great frequency difference observed here one can assume that the two calls are used for different distances. Because of the frequency-dependent attenuation the range of the low calls is considerably longer than that of the high. At 25 °C and 25 % rel. humidity the atmospheric attenuation amounts to 1.2 dB/m for 40 kHz, but only to 0.7 dB/m for 32 kHz (LAWRENCE and SIMMONS 1982). The low frequency calls accordingly range at the maximum about 30 m compared with 20 m of the high calls (110 dB SPL call amplitude, an ideal, large reflector and a hearing threshold of 0 dB SPL; according to LAWRENCE and SIMMONS 1982).

This hypothesis is supported by the distribution of the call intervals (fig. 2). In contrast to similar sized *Tylonycteris robustula* here the side peak at longer intervals is much more prominent. A slight error, however, may result from the fact that from distant animals only low calls could be recorded. But if the intervals between low and high calls are examined separately, one finds that additionally to the alternating use high calls are emitted in short intervals (e.g. during take-off), which correspond well to the call intervals in *Tylonycteris robustula* (fig. 2) and in other small Vespertilionini (AHLEN 1981). Between
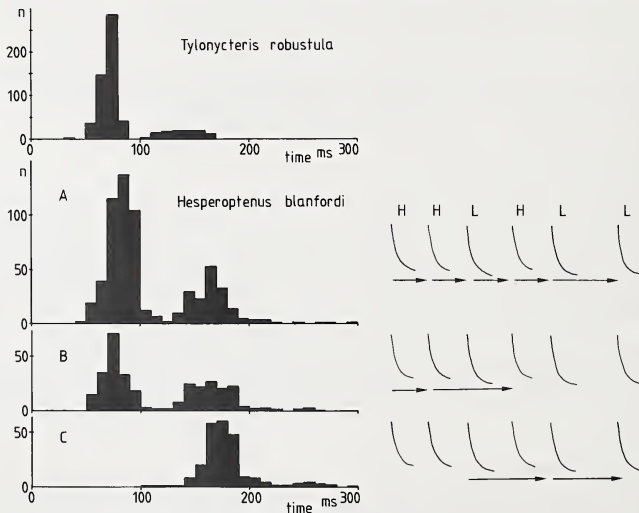

Fig. 2. Call intervals in *Tylonycteris robustula* (625 intervals, 20 sequences, 16 animals) and *Hespero- ptenus blanfordi* (618 intervals, 13 sequences, 11 animals). A: intervals irrespectivly of call structure; B: intervals exclusively between high frequency calls; C: intervals exclusively between low frequency calls. At the right the different intervals are indicated schematically by arrows (H: high frequency call, L: low frequency call)

two low calls, however, there is always a long interval (fig. 2C). In some cases it was evident that the expected high call between two low pulses was missing.

The frequency of the low calls of *Hesperoptenus blanfordi* is unusually low for its body size. The species lies in weight and condylobasal length between *Tylonycteris pachypus* and *Glischropus tylopus* on the one hand and *Tylonycteris robustula* on the other hand. Assuming a similar correlation between body size and call frequency as in the European Vespertilioni (WEID and v. HELVERSEN in prep.) and using the above mentioned species, a call frequency of about 40 kHz has to be expected. The same value is obtained, when the frequency is calculated by using condylobasal lengths and call frequencies of the European Vespertilionini (WEID and v. HELVERSEN 1987). The extraordinary low calls with their long range have also late returning echoes (maximum: 180 ms for 30 m).

For interpretation of these results one has to consider the echolocation system of vespertilionid bats. The animals are confronted with some difficulties in echo recognition. First, they must avoid that the echo returns during the emission of the call. Therefore they shorten their calls when approaching prey or obstacles (e.g. NEUWEILER 1984). In the same situation, however, they increase the call rate for exact localisation. A similar problem arises, when the echo returns very late thus interfering with the next call. Perhaps frequencies other than those emitted can be perceived during calling as is the case in Rhinolophidae (NEUWEILER 1970). If the echo returns even later, the bat has to assign the echoes to the respective calls. In the last mentioned cases successive calls with different frequencies will be helpful.

Through alternating, *Hesperoptenus blanfordi* could thus combine the advantages of long ranging calls with the better target recognition of high frequency calls and of a fast pulse repetition rate (combining thus the strategies of *Lasionycteris noctivagans* and *Lasiurus cinereus* [BARCLAY 1986]). It only has to make sure that echoes of low frequency calls do not interfere with calls of the same type. The different cf-parts carrying most sound energy allow a reliable assignment of echoes and respective calls.

A hypothesis to the foraging behaviour could imply that *H. blanfordi* can detect large prey for which it is possibly spezialized (HELLER and VOLLETH 1988) over great distances. With the high frequency calls it keeps in "ear" its closer surroundings. There are no indications to substantiate the considerations of GRIFFIN (1971) who says that the call frequency is related to the acoustical contact to earth or to the height above ground. Accordingly *Hesperoptenus blanfordi* should fly especially high. The aspect ration index, a wing dimension that is correlated with flight velocity and altitude (HABERSETZER 1986) is lower than in *Tylonycteris robustula* (HELLER in prep.). Also, the low frequency calls are emitted in low altitude as well.

Myotis hasseltii (Temminck, 1840)

The species which forages closely to the water surface shows steeply frequency-modulated calls without any cf component. The calls (duration 2,5–5,5 ms) start at about 82–104 kHz and sweep down to 23–30 kHz (fig. 1E). They correspond thus very well with those of the closely related and ecologically very similar *Myotis adversus* (THOMPSON and FENTON 1982). Additionally to the fundamental the first harmonic can frequently be observed.

The envelope of a call often shows several minima as is observed in other species hunting closely to the water surface (e.g. AHLEN 1981). They most probably result from interferences at the microphone between the echo from the water surface and the call. In otherwise similar calls of an animal flying above ground (after releasing) where the echos are considerably weaker those minima could not be found.

Family Emballonuridae

Emballonura monticola (Temminck, 1838)

The attribution of the calls described here to *Emballonura monticola* is not verified by observations of identified animals. The peculiar call structure, however, excludes all other Malaysian species with great certainty. The characteristic frequency pattern – a slight increase is followed by a part decreasing very slowly at first and more steeply later on – indicates an emballonurid bat. In no other family such calls are known. From the four Malaysian species the three *Taphozous* can be ruled out because of their totally different calls (see below). *Emballonura monticola*, which is commonly found in Ulu Gombak, is thus the only remaining species.

Duration (6–8 ms) and frequency pattern of all recorded calls are very uniform except for the final buzzes. The highest frequency which can here be exactly determined lies between 48 and 51 kHz (fig. 3A). In contrast to the Vespertilionidae, the first harmonic is most accentuated, the fundamental can sometimes weakly be seen. More often the third and the weaker second harmonic are observed (in not overmodulated records). In the final buzz (fig. 3D) the narrow frequency range is only slightly enlarged. Sometimes here the fundamental is more pronounced.
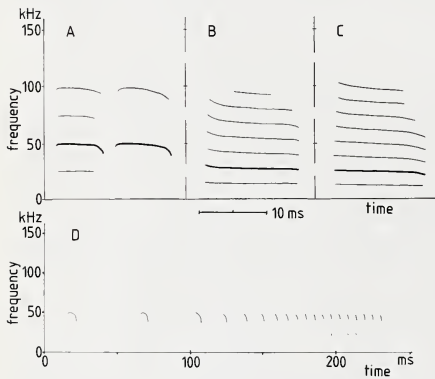

Fig. 3. Single echolocation calls of A: *Emballonura monticola*; B: *Taphozous melanopogon*; C: *Taphozous saccolaimus*; D: feeding buzz of *Emballonura monticola*
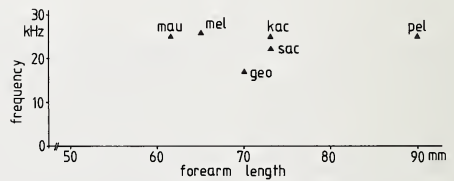
Fig. 4. Call frequency and forearm length in several *Taphozous* species (geo = *georgianus*: Fenton 1982; kac = *kachensis*: Neuweiler 1983, Habersetzer 1986; mau = *mauritianus*: Fenton et al. 1980; mel = *melanopogon*: Neuweiler 1983, Habersetzer 1986, this study; pel = *peli*: Pye 1980; sac = *saccolaimus*; forearm lengths according to Kingdon 1974, Habersetzer 1986, Heller and Volleth 1988, Strahan 1983

Genus *Taphozous*

The calls of the two *Taphozous* species *T. melanopogon* and *T. saccolaimus* are very similar in structure. Free flying, they both emit nearly constant frequency signals, which contain many harmonics known from other species of the genus (Pye 1980; Fenton 1982; Neuweiler 1983; Habersetzer 1986; only Fenton [1982] did not observe any harmonics). As in *Emballonura monticola* the first harmonic is the strongest component, the fundamental can often be weakly discerned, the upper harmonics decrease in amplitude corresponding to their number.

Comparing the call frequencies of the six *Taphozous* species studied so far one is surprised to see that there is no correlation to body size (fig. 4; forearm length used as measurement of body size; $y = 22.33 + 0.01x$; $r = 0.04$). This is in striking contrast to rhinolophid bats (genera *Rhinolophus* and *Hipposideros*; Heller and v. Helversen in prep.), several genera of vespertilionids (Weid and v. Helversen in prep.) and other
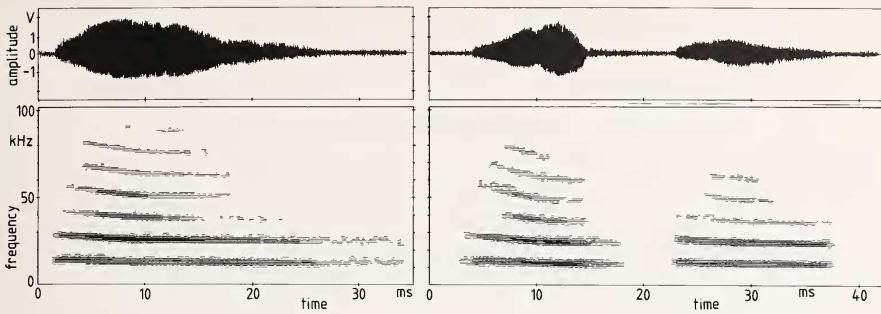
Fig. 5. Social calls of *Taphozous saccolaimus*. Notice the prominent fundamental

genera mentioned by Novick (1977). All these groups show a negative correlation between call frequency and body size (or forearm length). In the fast and high flying *Taphozous* body size apparently has less influence on echolocation than in the above mentioned genera.

Taphozous melanopogon Temminck, 1841

The species was recorded leaving the Batu Caves in the evening. The calls (duration 6–14 ms, rarely up to 17 ms) start at 26–30 kHz (first harmonic) and end with 24–26 kHz (average frequency drop 2 kHz; fig. 3B). In short calls occasionally a larger frequency range (31,5–23 kHz) is found and accordingly a steeper decrease. The call frequencies correspond well with the data of Neuweiler (1983) and Habersetzer (1986), the steep start and end components, however, mentioned by these authors are observed only very rarely.

Taphozous saccolaimus Temminck, 1838

The species was recorded leaving a hollow palm in the evening. The calls (duration mostly 8–14 ms, rarely 6–17 ms) start at 23–26 kHz (first harmonic) and sweep down to 20–24(–25) kHz (average frequency drop 2 kHz; fig. 3C).

Before taking off one animal emitted a series of social calls (fig. 5). They were similar to the echolocation calls but had a considerably more pronounced fundamental. The calls were composed of one or two elements, which were either clearly separated or fused (with a slight frequency increase in the central part).

Acknowledgements

Zusammenfassung

Ortungsrufe malayischer Fledermäuse

Die Ortungsrufe freifliegender Fledermäuse aus den Gattungen *Tylonycteris, Glischropus, Hesperopte-nus, Myotis, Emballonura* und *Taphozous* wurden im Feld aufgenommen und hinsichtlich Frequenz-zusammensetzung und -verlauf untersucht (Abb. 1, 3). Abgesehen von *Myotis hasseltii* (vollständig frequenzmodulierte Laute) bestehen die Rufe der Vespertilioniden aus einem frequenzmodulierten Anfangsteil und einem fast konstantfrequentem Ende (fm-cf-Rufe). *Hesperoptenus blanfordi* stößt dabei alternierend Rufe mit verschieden hohen cf-Teilen aus (32 und 40 kHz). Die Funktion dieses Verhaltens wird besonders im Hinblick auf die Reichweite des Echoortungssystems diskutiert. Die Arten der Gattung *Taphozous* zeigen wie alle bisher untersuchten Vertreter dieser Gattung fast

konstantfrequente Rufe, in denen neben der amplitudenstärksten 1. Harmonischen oft auch die Grundschwingung sowie höherzahlige Oberwellen deutlich zu erkennen sind. Die Rufe von *Emballonura monticula* sind ebenfalls nur schwach frequenzmoduliert.

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